Sex-biased parental care and sexual size dimorphism in a provisioning arthropod

Jeremy Field[1], Gavin Shreeves[2], Martyn Kennedy[3], Selina Brace[4] & James D. J. Gilbert[1,5]

[1]School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9GQ, UK

[2]Department of Medical Oncology, Mount Vernon Hospital, Rickmansworth Road, Northwood, Middlesex HA6 2RN, UK

[3]Allan Wilson Centre, Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand

[4]Department of Earth Sciences, Natural History Museum, London, SW7 5BD, UK

[5]Department of Biological, Biomedical and Environmental Science, University of Hull, Hull HU6 7RX, UK

*To whom correspondence should be addressed. Email: j.field@sussex.ac.uk. Telephone: +44 1273 877135.

The final publication is available at Springer via http://dx.doi.org/10.1007/s00265-015-2002-1

Abstract

The diverse selection pressures driving the evolution of sexual size dimorphism (SSD) have long been debated. While the balance between fecundity- and sexual selection has received much attention, explanations based on sex-specific ecology have proven harder to test. In ectotherms, females are typically larger than males, and this is frequently thought to be because size constrains female fecundity more than it constrains male mating success. However, SSD could additionally reflect maternal care strategies. Under this hypothesis, females are relatively larger where reproduction requires greater maximum maternal effort – for example where mothers transport heavy provisions to nests.

To test this hypothesis we focussed on digger wasps (Hymenoptera: Ammophilini), a relatively homogeneous group in which only females provision offspring. In some species, a single large prey item, up to 10 times the mother's weight, must be carried to each burrow on foot; other species provide many small prey, each flown individually to the nest.

We found more pronounced female-biased SSD in species where females carry single, heavy prey. More generally, SSD was negatively correlated with numbers of prey provided per offspring. Females provisioning multiple small items had longer wings and thoraxes, probably because smaller prey are carried in flight.

Despite much theorising, few empirical studies have tested how sex-biased parental care can affect SSD. Our study reveals that such costs can be associated with the evolution of dimorphism, and this should be investigated in other clades where parental care costs differ between sexes and species.

Keywords: Sexual dimorphism, Parental care, Hymenoptera, Wasps

Introduction

Sexual dimorphism is ubiquitous. Males and females normally use different strategies to optimize their fitnesses, and therefore differ in their optimum trait values. Dimorphism is therefore expected to evolve, although it may be constrained by genetic correlations between the sexes (Lande 1980; Chippendale et al. 2001). One of the most obvious examples of dimorphism is sexual size dimorphism (SSD). In birds and mammals, SSD is commonly male-biased, whereas in invertebrates and other ectotherms, it is females that are typically larger than males (e.g. Clutton-Brock et al. 1977; Berry and Shine 1980; Gilbert 1983; O'Neill 1985; Hurlbutt 1987; Nylin and Wedell 1994; Head 1995; Fairbairn 1997; Lindenfors et al. 2002; Blanckenhorn et al. 2007). Whether SSD is male- or female-biased is thought to result from (1) differences in sex-specific patterns of sexual selection, typically on males, versus fecundity selection, typically on females (Fairbairn et al 2007); and (2) sex-specific ecological selection pressures, such as intersexual competition for resources (e.g. Ralls 1976; Herrel et al 1999) or differences in the reproductive roles of the two sexes (e.g. Myers 1978). The latter hypothesis, concerning sex-specific reproductive roles, is known as the dimorphic niche hypothesis (Ralls 1976; Shine 1989; reviewed in Hedrick & Temeles 1989). The relative importance of the different explanations for variation in SSD remains unclear (e.g. Ralls 1976; Hedrick & Temeles 1989; Shine 1989; Nylin and Wedell 1994; Blanckenhorn 2005; Cox 2006; del Castillo & Fairbairn 2011). Unambiguous evidence for ecological factors affecting size dimorphism are mainly confined to within-species studies of feeding morphology (Temeles et al 2008, but see Reimchen & Nosil 2004), while broad comparative studies often make it difficult to disentangle the effects of

diverse reproductive traits (e.g. Han & Fu 2013, but see Stephens & Wiens 2009).

In arthropods, females are usually larger than males, although the extent of SSD varies, and a minority of taxa exhibit male biased SSD (Andersson 1994; Fairbairn et al 2007; Stillwell et al 2010). One possible explanation for the prevalence of female-biased SSD in arthropods is based on patterns of sexual- versus fecundity selection as outlined above. Specifically, the inflexibility of the arthropod exoskeleton will limit female ovary size and egg number (Stearns 1977), suggesting that dimorphism may result from stronger effects of body size on female fecundity than on the mating success of males (Ralls 1976; Head 1995). Others have instead argued that patterns of sexual selection on males alone may drive both male- and female-biased SSD (Fairbairn and Preziozi 1994; see also Preziozi & Fairbairn 2000). In this paper, however, we focus on an ecological explanation for variation in SSD in line with the dimorphic niche hypothesis: variation in the costs of maternal care. Parental care is well known to be extremely costly in arthropods (e.g. Hunt et al 2002), and is nearly always carried out by females only (Costa 2006; Trumbo 2012; Gilbert & Manica 2015). Care involves diverse behaviours such as constructing nests; gathering and defending resources; and transporting, provisioning and defending offspring (Hinton 1981; Choe & Crespi 1997; Costa 2006). Larger individuals are likely to have an advantage in carrying out many of these behaviours. Our hypothesis is that females should be relatively larger where reproduction requires periods of greater maximum size-dependent effort. Size-dependent effort might select for larger females where larger females experience reduced costs when building nests (e.g. gathering and packing breeding resources such as dung masses; Hunt et al 2002) or when defending offspring or nesting resources against larger or

physically stronger enemies (e.g., Goubault et al. 2007). The specific hypothesis we focus on, however, is that females should be relatively larger when they have to transport all of the food that an offspring will require in a single load, such that the maximum effort required is relatively high. Females should be progressively smaller as they are able to divide food into multiple, smaller loads that each require less effort.

Shreeves and Field (2008) used a comparative analysis to show that, in wasps and bees, where only females provide parental care, the degree of dimorphism is correlated with parental care strategies. Provisioning taxa, in which females must construct and provision nests, showed consistently more female-biased size dimorphism than cuckoo-parasitic taxa, in which females do not provision, but instead oviposit in the nests of provisioning taxa. Shreeves and Field (2008) suggested two possible explanations for this pattern. The first was that if nest construction is physically demanding (e.g. digging a burrow in hard soil), there might be selection for increased female size in provisioning taxa compared with cuckoo parasites, which do not construct nests. In support of this explanation, those provisioning taxa in which construction costs may be minimized, because females nest in pre-existing cavities, tended to have less female-biased SSD than taxa where females construct their own nests. This pattern was not significant, however, after controlling for phylogeny, although the sample size available was small.

The second explanation, which could operate simultaneously with the first, was that the demands of transporting provisions to the nest select for larger size (see also Coelho 1997). This would again result in more female-biased dimorphism in provisioners than cuckoo parasites, since only females transport provisions. In support of this idea, Shreeves and Field (2008) found that pompilid wasps, which provision each offspring with a single relatively large prey item, exhibited more female-biased size

148 dimorphism than apoid wasps, in which each offspring is usually
149 provided with several smaller items that are carried individually to the
150 nest so that the maximum level of effort required is presumably smaller.
151 Bees, in which provisions are tiny pollen grains, showed the least
152 dimorphism. There are, however, other explanations for these results
153 (Shreeves and Field 2008). For example, pompilids were also the only
154 taxa in the analysis that prey exclusively on spiders. Spiders are normally
155 larger than the female wasp, and may be particularly dangerous and
156 difficult to hunt, potentially providing an alternative explanation for
157 larger female size in pompilids. In this paper, we carry out a better
158 controlled test of the hypothesis that SSD is correlated with the costs of
159 transporting provisions, by examining a single, monophyletic lineage of
160 provisioners in which provision weight varies interspecifically. We thus
161 provide a rare comparative test of the dimorphic niche hypothesis.
162 Ammophiline digger wasps (Apoidea: Sphecidae, Ammophilini)
163 are particularly well suited to a test of the dimorphic niche hypothesis.
164 There is a recently derived molecular phylogeny for ammophilines (Field
165 et al. 2011), and in one species that provides multiple prey items per
166 offspring, experimental fieldwork has shown that provisioning is costly in
167 terms of lifetime reproductive success (Field et al. 2007). Furthermore,
168 whilst most of the species' ecology is largely similar across the tribe,
169 there is considerable interspecific variation in the likely maximum costs
170 involved in transporting offspring food. Some ammophilines provision
171 each offspring with only a single, large prey item, which can be 10 times
172 the weight of the transporting female parent (e.g. Weaving 1989a; Field,
173 1992a, 1993). In contrast, other species provide each offspring with up to
174 ten or more individually smaller prey, which are carried to the nest one at
175 a time (e.g. Kazenas 1971; Weaving 1989a; Field *et al.* 2007). Detailed
176 studies of individual species suggest that providing offspring with

multiple prey (1) gives mothers finer control over offspring size but (2) may lead to more prey theft from nests by conspecifics (Field 1992a) and (3) may or may not influence the frequency of natural enemy parasitism (Rosenheim 1989; Field 1992a). Here, we carry out a phylogenetically-controlled test of the hypothesis that provisioning with individually larger prey requires greater maximum size-dependent effort and therefore selects for more female-biased SSD.

Natural history of ammophiline wasps

Ammophilines exhibit little interspecific variation in terms of gross morphology: they are relatively large wasps with long thin abdomens. While prey size varies interspecifically, ammophilines are otherwise also relatively homogeneous ecologically. Nests of all species are short burrows dug in the ground, each containing a single offspring. The wasp larva feeds on the prey provided by its mother, then pupates in the nest. Detailed studies of individually marked *A. pubescens* (J. Field & W.A. Foster, in prep.) and *A. sabulosa* (Field 1992a) show that long-lived females may provision 10-20 different offspring in their lives. A few species are progressive provisioners, and maintain more than one nest simultaneously (including 4 species in this study: *E. dives* and *Ammophila azteca, pubescens* and *rubiginosa*). In nearly all taxa, prey are lepidopteran caterpillars which are paralysed by the mother's sting, an exception being *Eremochares dives* which preys on immature Orthoptera (Kazenas 1971). Most species appear to be generalists in terms of prey species (e.g. Evans 1959; Weaving 1988; Field 1992b). Although male mating tactics have been little studied, there is no evidence of major variation, such as male territoriality, that could affect optimal male size.

Aside from prey size, one source of variation that could conceivably influence optimum female size and hence sexual dimorphism in ammophilines is variation in the method of prey carriage and its effect upon transport costs (e.g. Marden 1987, Lighton et al. 1993). In ammophilines that provide each offspring with a single large prey item, mothers carry their prey to the nest on foot, held off the ground using their mandibles and fore-legs. In contrast, species that provide several smaller prey per offspring typically fly with their prey, and in species in which prey size varies, females often carry large prey on foot, intermediate prey in short hopping flights, and small prey in longer flights (e.g. Field 1992a; see also Table 1 in Powell 1964). The relative costs of carriage in flight versus carriage on foot are not known, but flight is likely to be costlier for a given prey size. If so, species that fly with prey would be expected to be more dimorphic, acting against our main hypothesis and making this study a conservative test of our main prediction.

Methods

Data collection

We obtained data for as many ammophilines as possible for which there are published prey size data, among the 40 species included in the molecular phylogeny of Field et al. (2011). Absolute prey size is rarely reported in the literature, but a sample of nests is typically opened and the number of prey provided per offspring recorded. Since most species provision the full complement of prey before their egg even hatches, all prey are available to be counted at the same time. The prey provided to a larva constitute the only food available to it before adulthood, so that there is likely to be a strong correlation between total provision weight and resulting adult offspring weight (e.g. Field 1992a; J. Field, unpubl

data). The number of prey per offspring (PPO) thus provides an estimate of prey size relative to female size which is ideal for our purposes: the more prey per offspring, the relatively smaller the prey must be. Indeed, this relationship is observed intraspecifically in *A. sabulosa*: total prey weight provided to offspring was constant across nests, because of a strongly inverse relationship between prey number and individual prey size (Field 1992a; studies of non-ammophiline wasps that report similar relationships are referenced therein). In the literature, only the observed PPO range across the nests in a population is reported for every species, and we therefore used the midpoint of this range ((maximum PO + minimum PPO)/2 :see Table 1).

Morphometric data came from specimens loaned from museums, the first author's own collections, and from samples kindly sent by private collectors and by the authors of published studies that report PPO. Three measurements were taken from each specimen. The first was thorax length, estimated as the length of the scutum excluding the extended posterior lip that occurs in some species. The second measurement was right forewing length, estimated as the distance between (1) the inner edge of the wing veins forming the proximal corner of submarginal cell 1 and (2) the inner edge of the wing veins forming the distal corner of the marginal cell. Thorax and wing terminology refer to Bohart and Menke (1976, Figures 2a and 5). These two metrics were chosen because they could be located in all species, and because they relate to a female's ability to fly with a load. Longer wings, and a larger thorax allowing a larger flight muscle mass, should both allow more lift to be generated (Marden 1987). Measurements were made to the nearest 0.05mm using a Leica MZ6 binocular microscope equipped with an eyepiece graticule.

Our third metric, intended to reflect overall body size, was dry weight. Pinned specimens were dried by placing them in an oven at 70ºC for 48 hours, preliminary studies having shown that dry weight did not change detectably after 24 hours. After 48 hours, each specimen was removed from the oven and immediately weighed, including the pin, on a Sartorius balance to 0.0001g. The specimen was then relaxed so that it was no longer brittle, by keeping it in a humid atmosphere overnight. After relaxing, it was carefully removed from its pin, and the pin alone weighed after drying. Specimen dry weight was obtained by subtracting pin weight from the combined weight of pin+wasp. Specimens were then repinned intact. Preliminary work suggested that the relationship between dry weight and thorax or wing length might be altered in the minority of specimens that had been stored in alcohol, and we therefore did not weigh these. For this reason, and because we did not want to risk damaging old museum specimens by removing them from their pins (Gilbert 2011), the sample size for dry weight was often smaller than for thorax or wing length.

The same person carried out all measurements for a given metric, and measurement error, estimated by blind re-measurement of a sample of 25 specimens, was 1.3%, 0.7%, and 2.7% for thorax, wing and weight, respectively. Table 1 summarizes the data sources.

Statistical analysis

A species was included in the analysis only if at least five specimens of each sex were available for each of the three morphometrics. This allowed 21 species to be included, from five genera: *Ammophila* (16 species), *Podalonia* (2 species), *Eremnophila* (one species), *Eremochares*

(one species) and *Hoplammophila* (one species) (Table 1). All morphological variables were $\log_{10}$-transformed before analysis. For a given total weight of prey provided to an offspring, the weight of individual prey should be proportional to 1/n, where n is the number of prey provided. If female weight is proportional to individual prey weight according to our hypothesis, the expected relationship between PPO and female weight or weight dimorphism would be exponential, but linearized by log transformation.

To analyse the data incorporating evolutionary relationships, we used Phylogenetic Generalised Least Squares (PGLS) models fitted using the R package caper (Orme et al 2012) and using the phylogeny given in Field et al (2011). For example, to test whether PPO was correlated with sexual dimorphism, the dependent variable was log(mean female weight), with log(mean male weight), PPO, and their interaction as potential explanatory variables (e.g. Ranta et al. 1994; Shreeves and Field 2008). We used a reverse stepwise procedure to test the significance of each model term, using likelihood ratio tests (distributed as chi-squared) as a criterion for model selection.

Results

Sexual size dimorphism and relative prey size

The phylogeny used in this study, along with extant character states used in our analyses and their reconstructed ancestral states, are given in Fig. 1. Across species, the weights of the two sexes were strongly correlated, with females always heavier than males. When we treated PPO as a binary variable (i.e. single vs. multiple prey items), species provisioning

single, relatively large prey items had significantly heavier females for a given male weight than did species provisioning multiple, relatively smaller prey items (PGLS, dropping "PPO", LR=10.81, df=1, p=0.001; Fig. 2). Multiple prey items did not affect the slope of the relationship between female and male weight (dropping the "PPO x male weight" interaction, LR=2.18, df=1, p=0.139; Fig. 2).

Treated as a scalar count variable, PPO was also negatively associated with female weight even after accounting for male weight (PGLS, LR=6.77, df=1, p=0.009), but again was not associated with the slope of the relationship between male and female weight (PGLS, dropping the "PPO x male weight" interaction, LR=1.92, df=1, p=0.166).

Sexual size dimorphism (untransformed female weight/male weight) based on dry weight varied from 1.18 to 2.96 among the 21 species included in the analysis. Using this ratio as a response variable, "dimorphism", there was a negative relationship between dimorphism and PPO: species that capture relatively fewer prey were more dimorphic (PGLS, LR=5.10, df=1, p=0.023; Fig. 3). Note that residuals for this model were slightly non-normal owing to two outliers (*A. wrightii*, *P. affinis*); removing these outliers to normalize residuals had no qualitative effect on the result (PGLS, outliers removed: n=19, LR=4.56, df=1, p=0.033).

Wing and thorax length

After accounting for dry weight, females of species that capture relatively small prey (high PPO) had relatively long wings and thoraxes (PGLS; wing: LR=8.85, df=1, p=0.003; thorax: LR=14.22, df=1, p<0.001; Fig 3a,

b). There was no interaction between PPO and dry weight in either case (PGLS, both NS). For males, PPO was associated with neither wing nor thorax length (PGLS; wing: LR=0.60, df=1, p=0.438; thorax: LR=1.89, df=1, p=0.168; Fig. 4c, d).

Discussion

Our findings are consistent with the dimorphic niche hypothesis, which states that sex-specific ecological selection pressures drive patterns of SSD (Ralls 1976). Only female digger wasps provision offspring, and in species with relatively larger prey which presumably each require more effort to handle and transport, we found that females are relatively larger compared with conspecific males. These results are in turn consistent with Shreeves & Field's (2008) suggestion that the demands of female parental care might explain why provisioning taxa in general have more female-biased SSD than non-provisioning taxa such as cuckoo parasites. Shreeves & Field (2008) provided some evidence in support of their idea, but could not completely discount competing explanations based on other potential differences between provisioning and non-provisioning taxa. Most of these differences are avoided in the present analysis, where we have focused on a single, relatively homogeneous lineage. We now consider factors other than prey size that could potentially influence SSD in ammophilines, then discuss evidence that the demands of parental care influence dimorphism in other taxa.

The correlation we have found between relative prey size and SSD does not indicate direction of causation. It is possible that variation in factors other than prey size drives SSD, and that SSD in turn drives prey size selection. However, while differences in the physical demands of prey carriage are unlikely to be the sole ecological factor driving interspecific variation in ammophiline SSD, there is currently little evidence for significant variation in other factors. Such factors might include differences in fecundity, differences in the demands of nest construction and prey capture, and the possibility that females of some species are more likely to fight over burrows and prey, perhaps depending

384 on female density (e.g. Parker et al. 1980). Differences in the hardness of
385 the nesting substrate could be important if they affect the demands of nest
386 construction. However, most ammophilines nest in relatively soft, sandy
387 soil, although at least one species not included in our analyses uses harder
388 substrates (Weaving 1989b). Interestingly, SSD appeared to be more
389 variable among species that provide only a single large prey item per
390 offspring than among species that provide several small prey (Fig. 3).
391 This might partly be because species that provide only a single large prey
392 item have less fine control over offspring size, which will depend largely
393 on the size of the single prey (Field 1992a). In addition, however, the
394 species in our analysis that provide only a single prey item come from
395 four different genera, whereas 9 of the 10 multiple-prey species are from
396 the same genus (Table 1): differences in dimorphism may thus partly
397 reflect common ancestry, although we have to an extent controlled for
398 this by using phylogenetic analysis.
399 Our findings concerning wing and thorax morphology provide
400 further evidence that relative prey size influences sexual dimorphism. We
401 found that ammophiline species capturing relatively smaller prey that are
402 more likely to be carried in flight had longer wings and thoraxes for their
403 body weights than species that capture relatively large prey carried on
404 foot. These relationships were significant only for females, the prey-
405 carrying sex. Longer wings, and a larger thorax allowing larger flight
406 muscles, are both potential correlates of a greater load-carrying ability
407 while flying. Marden (1987) found that body mass, flight muscle mass
408 and wing size were all strongly positively correlated with maximum
409 experimentally liftable weight across a range of taxa, but that flight
410 muscle mass explained the most variation after controlling for body mass.
411 Our findings also suggest that the frequency of prey carriage in flight,
412 rather than the relative size of the individual prey carried, drives these

aspects of body shape: species with relatively smaller prey more often carry prey in flight, but the individual prey themselves are smaller in comparison with body weight. The costs of carrying a given weight of prey in flight versus on foot remain unquantified, but our results suggest that thorax and wing length may not always be ideal surrogates for overall body weight in morphometric analyses.

Mating systems are not known to vary among ammophiline species, although male behaviour has been little studied. Mating involves the male sitting astride the female, grasping her around the neck with his mandibles while contacting the tip of her abdomen with the genitalia at the tip of his own abdomen (J. Field, pers. obs.). The range of female sizes that is available as potential mates may therefore depend on a male's own body length; a shorter male might be unable to simultaneously grasp and mate with a larger female. It is therefore not surprising that body sizes of the two sexes are strongly correlated (Fig. 2), and it would be interesting to know whether males are longer and thinner in taxa where females are relatively large compared with males.

Although within-clade comparative tests are rare, evidence from a variety of taxa is consistent with the idea that the physical demands of carrying heavy loads can drive SSD. For example, male-biased size dimorphism is observed in several taxa where males carry females in nuptial flights (e.g. thynnine wasps, caddisflies: Evans 1969; Petersson 1995; O'Neill 2001). In terms of parental care, male belostomatine bugs exhibit sex role reversal, with the male providing parental care via back-brooding. Accordingly belostomatines also display male-biased size dimorphism, reflecting the demands of carrying and aerating the eggs (Iglesias et al 2012). In vespertilionid bats, females carry embryos weighing up to 30% of their own body weight, and also transport young after birth. As expected, Myers (1978) found that SSD was greater in

species where a greater total weight of young is carried. Less clear-cut is the female-biased size dimorphism in birds of prey, which contrasts with the male-biased dimorphism typical for birds in general. Selection on foraging ability was initially thought to favour larger female birds of prey (Wheeler and Greenwood 1983), but in fact may instead select for smaller males according to more recent studies (Tornberg et al. 1999; Krüger 2005; Weimerskirch et al. 2006). However, in hawk owls (*Ninox* spp.), some species show a reversed pattern in which males are larger. In these species, breeding males show "prey-holding behaviour" whereby males capture and hold a single large prey item for a whole day without consuming it, a behaviour that has been implicated in selection for large male size (Pavey 2008).

Although the demands of parental care have the potential to drive patterns of sexual dimorphism in provisioning taxa, this may depend on mothers being able to determine offspring sex directly, so that the sex that cares for offspring can be provided with more food during development. Hymenopteran females do indeed have direct control over the sex of individual offspring. Mechanistically, a more female-biased size dimorphism in taxa that capture larger prey is presumably achieved through mothers having a higher threshold total provision weight above which they lay female eggs. In both scarabaeid and silphid beetles, male involvement in nest-building and parental care varies among species (Halffter et al 1997, Costa 2006). As a hypothesis for future study, the relative disparity between male and female parental effort might also be predicted to affect size dimorphism in these taxa. Indeed, some scarabaeines provision their offspring in discrete chambers analogous to the cells of ammophilines (e.g. Monteith & Storey 1981; Edwards & Aschenborn 1989; Favila 1993; Halffter 1997). However, direct control

of offspring sex may be absent in scarabaeines, potentially constraining the evolution of sexual size dimorphism.

Acknowledgements

We thank Charlotte Stimmler, who performed some of the measurements, and T. Collett, E. Leadbeater, J. Green, E. Lucas and C. Bridge for comments on an earlier version of the manuscript. We also thank J.D. Asis, Y. Barbier, P. Gambino, A.W. Hook, V.L. Kazenas, R.P. Martins, A.S. Menke, M.F. O'Brien, A.M O'Brien, F.D. Parker, J.A. Rosenheim, V.J. Tepedino and A.J.S. Weaving for kindly giving access to specimens used in the study.

Compliance with ethical standards

The authors declare that they have no conflict of interest. This article does not contain any studies with human participants or animals performed by any of the authors.

References

Andersson M (1994). Sexual Selection. Princeton University Press, Princeton.

Baerends GP (1941) Fortpflanzungsverhalten und orientierung der grabwespe *Ammophila campestris* Jur. Tijdschr. voor Entomol. 84:68-275

Berry JF, Shine R (1980) Sexual size dimorphism and sexual selection in turtles (order Testudines). Oecologia 44:185-191

Blanckenhorn WU (2005) Behavioral Causes and Consequences of Sexual Size Dimorphism. Ethology 111: 977-1016

Blanckenhorn WU, Dixon AFG, Fairbairn DJ, Foellmer MW, Gibert P, van der Linde K, Meier R, Nylin S, Pitnick S, Schoff C, Signorelli M, Teder T, Wiklund C (2007) Proximate causes of Rensch's rule: Does sexual size dimorphism in arthropods result from sex differences in development time? Am. Nat. 169:245-257

Blösch M (2000) Die Grabwespen Deutschlands. Goecke & Evers, Keltern

Bohart RM, Menke AS (1976) Sphecid Wasps of the World: a generic revision. Univ. California Press, Berkeley

del Castillo RC, Fairbairn, DJ (2012) Macroevolutionary patterns of bumblebee body size: detecting the interplay between natural and sexual selection. Ecol. Evol. 2(1): 46-57

Chippendale AK, Gibson JR, Rice WR (2001) Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. P. Natl. Acad. Sci. USA, 98(4): 1671-5

Choe JC, Crespi BJ (eds) (1997) *The evolution of social behaviour in insects and arachnids.* Cambridge University Press.

516 Clutton-Brock TH, Harvey PH, Rudder B (1977) Sexual size
517 dimorphism, socionomic sex ratio and body weight in primates. Nature
518 269:797-800
519 Coelho JR (1997) Sexual size dimorphism and flight behavior in cicada
520 killers (*Sphecius speciosus*). Oikos 79:371-375
521 Costa JC (2006) The other insect societies. Belknap/Harvard, Cambridge
522 MA.
523 Cox RM (2006) A test of the reproductive cost hypothesis for sexual size
524 dimorphism in Yarrow's spiny lizard *Sceloporus jarrovii*. J. Anim.
525 Ecol. 75(6): 1361-1369
526 De Groot W (1974) Een in kevergaten nestelende *Ammophila*, *A. clypeata*
527 (Hym., Sphecidae). Entomol. Ber. 34:24-28
528 Dollfuss H (2015) Revision of the wasp genus *Ammophila* KIRBY 1798
529 (Hymenoptera: Apoidea: Sphecidae) of the Sub-Saharan Region of
530 Africa. Linzer Biol. Beiträge 47:307-412.
531 Edwards PB, Aschenborn HH (1989). Maternal care of a single offspring
532 in the dung beetle *Kheper nigroaeneus*: the consequences of extreme
533 parental investment. J. Nat. Hist., 23(1): 17-27
534 Evans HE (1959) Observations on the nesting behavior of digger wasps
535 of the genus *Ammophila*. Am. Midl. Nat. 62:449-473
536 Evans HE (1965) Simultaneous care of more than one nest by *Ammophila*
537 *azteca* Cameron (Hymenoptera: Sphecidae). Psyche 72:8-23
538 Evans HE (1969) Phoretic copulation in the Hymenoptera. Ent. News
539 80:113-124
540 Fairbairn DJ (1997) Allometry for sexual size dimorphism: Pattern and
541 process in the coevolution of body size in males and females. Annu. Rev.
542 Ecol. Syst. 28:659-687

543 Fairbairn DJ, Preziozi RF (1994) Sexual selection and the evolution of
544 allometry for sexual size dimorphism in the water strider, *Aquarius*
545 *remigis*. Am. Nat. 144:101-118
546 Fairbairn DJ, Blanckenhorn WU, Szekely T (2007). Sex, Size and Gender
547 Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford
548 University Press, New York.
549 Favila ME (1993) Some ecological factors affecting the life-style of
550 *Canthon cyanellus cyanellus* (Coleoptera Scarabaeidae): an experimental
551 approach. Ethol. Ecol. Evol. 5(3): 319-328
552 Field J (1989) Intraspecific parasitism and nesting success in the solitary
553 wasp *Ammophila sabulosa*. Behaviour 110:23-45
554 Field J (1992a) Patterns of nest provisioning and parental investment in
555 the solitary digger wasp *Ammophila sabulosa*. Ecol. Entomol. 17:43-51
556 Field J (1992b) Prey utilization by the solitary digger wasp *Ammophila*
557 *sabulosa* (Linnaeus) (Hymenoptera: Sphecidae). Entomol. Gazette
558 43:131-138
559 Field J (1993) Nesting biology of the solitary digger wasp *Podalonia*
560 *affinis* (K.) (Hymenoptera: Sphecidae). Entomologist 112:17-24
561 Field J, Ohl M, Kennedy M (2011) A molecular phylogeny for digger
562 wasps in the tribe Ammophilini (Hymenoptera, Apoidea, Sphecidae).
563 Syst. Entomol. 36:732-740 doi:Doi 10.1111/J.1365-3113.2011.00591.X
564 Field J, Turner E, Fayle T, Foster WA (2007) Costs of egg-laying and
565 offspring provisioning: multifaceted parental investment in a digger
566 wasp. Proc. Roy. Soc. Lond. B 274:445-451 doi:Doi
567 10.1098/Rspb.2006.3745
568 Gaimari SD, Martins RP (1996) Nesting behavior and nest distributions
569 of *Ammophila gracilis* Lepeletier (Hymenoptera:
570 Sphecidae) in Brazil. J. Hymenopt. Res. 5:240-248

571 Gilbert JDJ (2011) Insect Dry Weight: Shortcut to a Difficult Quantity
572 using Museum Specimens. Fla. Entomol. 94(4): 964-970.
573 Gilbert JDJ, Manica A (2015) The evolution of parental care in insects: a
574 test of current hypotheses. Evolution 69(5): 1255-1270.
575 Gilbert JJ (1983) Sexual dimorphism in zooplankton (Copepoda,
576 Cladocera, and Rotifera). Annu. Rev. Ecol. Syst. 14:1-33
577 Goubault M, Scott D, Hardy IC (2007) The importance of offspring
578 value: maternal defence in parasitoid contests. Anim. Behav. 74(3): 437-
579 446.
580 Halffter G (1997) Subsocial behavior in Scarabaeinae beetles. In: Choe J,
581 Crespi BJ, eds. The evolution of social behavior in insects and arachnids.
582 Cambridge University Press, UK.
583 Han X, Fu J (2013). Does life history shape sexual size dimorphism in
584 anurans? A comparative analysis. BMC Evol. Biol. 13(1): 27.
585 Head G (1995) Selection on fecundity and variation in the degree of
586 sexual size dimorphism among spider species (class Araneae). Evolution
587 49:776-781
588 Hedrick AV, Temeles EJ (1989) The evolution of sexual dimorphism in
589 animals: hypotheses and tests. Trends Ecol. Evol. 4(5): 136-138.
590 Herrel A, Spithoven L, Van Damme R, De Vree F (1999) Sexual
591 dimorphism of head size in *Gallotia galloti*: testing the niche divergence
592 hypothesis by functional analyses. Funct. Ecol. 13(3), 289-297.
593 Hicks CH (1934) Biological notes on *Sphex wrightii* (Cresson). Psyche
594 41:150-157
595 Hinton HE (1981) *Biology of insect eggs*, Vol. 1. Pergamon Press,
596 Oxford.
597 Hunt J, Simmons LW, Kotiaho JS (2002) A cost of maternal care in the
598 dung beetle *Onthophagus taurus*? J. Evol. Biol. 15(1): 57-64.

599 Hurlbutt B (1987) Sexual size dimorphism in parasitoid wasps. Biol. J.
600 Linn. Soc. 30:63-89
601 Iglesias MS, Crespo FA, Valverde ADC (2012) Is parental care behavior
602 in *Belostoma* species an evolutionary cause for their common sexual size
603 dimorphism pattern? Ent. Sci. 15(2): 155-161
604 Kazenas VL (1971) The biology of the fossorial wasp *Ammophila*
605 (*Eremochares*) *dives* Brullé (Hymenoptera, Sphecidae). Entomol. Rev.
606 49:172-180
607 Krüger O (2005) The evolution of reversed sexual size dimorphism in
608 hawks, falcons and owls: a comparative study. Evol. Ecol. 19(5): 467-486
609 Kurczewski FE, Spofford MG (1998) Alternative nesting strategies in
610 *Ammophila urnaria* (Hymenoptera : Sphecidae). J. Nat. Hist. 32:99-106
611 Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in
612 polygenic characters. Evolution 34(2): 292-305
613 Lighton JR, Weier JA, Feener Jr DH. (1993) The energetics of
614 locomotion and load carriage in the desert harvester ant *Pogonomyrmex*
615 *rugosus*. J. Exp. Biol. 181:49-61
616 Lindenfors P, Tullberg BS, Biuw M (2002) Phylogenetic analyses of
617 sexual selection and sexual size dimorphism in pinnipeds. Behav. Ecol.
618 Sociobiol. 52:188-193
619 Lomholdt O (1984) The Sphecidae (Hymenoptera) of Fennoscandia and
620 Denmark. Fauna Entomologica Scandinavica vol 4 (2nd edition).
621 Scandinavian Science Press Limited, Denmark
622 Marden JH (1987) Maximum lift production during takeoff in flying
623 animals. J. Exp. Biol. 130:235-258
624 Monteith GB, Storey RI (1981) The biology of *Cephalodesmius*, a genus
625 of dung beetles which synthesizes "dung" from plant material
626 (Coleoptera: Scarabaeidae: Scarabaeinae). Mem. Qld. Mus. 20(2): 253-
627 277

628 Myers P (1978) Sexual dimorphism in size of vespertilionid bats. Am.
629 Nat. 112(986): 701-711
630 Nylin S, Wedell N (1994) Sexual size dimorphism and comparative
631 methods. In: Eggleton P, Vane-Wright RI (eds) Phylogenetics and
632 Ecology. Academic Press, London
633 O'Brien MF, O'Brien AM (1988) Biology of *Ammophila evansi* and *A.*
634 *mediata* in Northern Michigan (Hymenoptera: Sphecidae). Pan-Pac.
635 Entomol. 64:73-79
636 O'Neill KM (1985) Egg size, prey size and sexual size dimorphism in
637 digger wasps (Hymenoptera: Sphecidae). Can. J. Zool. 63:2187-2193
638 O'Neill KM (2001) Solitary wasps. Cornell University Press, Ithaca.
639 Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W
640 (2012) caper: Comparative Analyses of Phylogenetics and Evolution in
641 R. R package version 0.5. URL:http://CRAN.R-
642 project.org/package=caper
643 Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics
644 and evolution in R language. Bioinformatics 20: 289-290
645 Pavey CR (2008) Evolution of prey holding behaviour and large male
646 body size in *Ninox* owls (Strigidae). Biol. J. Linn. Soc. 95(2): 284-292
647 Parker FD, Tepedino VJ, Vincent DL (1980) Observations on the
648 provisioning behavior of *Ammophila aberti* Haldeman (Hymenoptera:
649 Sphecidae). Psyche 87:249-258
650 Petersson E (1995) Male load-lifting capacity and mating success in the
651 swarming caddis fly *Athripsodes cinereus*. Physiol. Ent. 20:66-70
652 Powell JA (1964) Additions to the knowledge of the nesting behavior of
653 North American *Ammophila* (Hymenoptera: Sphecidae). J. Kansas
654 Entomol. Soc. 37:240-258

655 Preziosi RF, Fairbairn DJ (2000) Lifetime selection on adult body size
656 and components of body size in a waterstrider: opposing selection and
657 maintenance of sexual size dimorphism. Evolution 54(2): 558-566.
658 Ralls K (1976) Mammals in which females are larger than males. Q. Rev.
659 Biol. 51:245-276
660 Ranta E, Laurila a, Elmberg J (1994) Reinventing the wheel - analysis of
661 sexual dimorphism in body size. Oikos 70:313-321
662 Reimchen TE, Nosil P (2004) Variable predation regimes predict the
663 evolution of sexual dimorphism in a population of threespine stickleback.
664 Evolution 58(6): 1274-1281
665 Rosenheim JA (1987) Nesting-Behavior and Bionomics of a Solitary
666 Ground-Nesting Wasp, *Ammophila dysmica* (Hymenoptera, Sphecidae) -
667 Influence of Parasite Pressure. Ann. Entomol. Soc. Am. 80:739-749
668 Rosenheim JA (1989) Behaviorally mediated spatial and temporal refuges
669 from a cleptoparasite, *Argochrysis armilla* (Hymenoptera, Chrysididae),
670 attacking a ground-nesting wasp, *Ammophila dysmica* (Hymenoptera,
671 Sphecidae). Behav. Ecol. Sociobiol. 25: 335-348.
672 Shine R (1989) Ecological Causes for the Evolution of Sexual
673 Dimorphism: A Review of the Evidence. Q. Rev. Biol. 64(4):419-461
674 Shreeves G, Field J (2008) Parental care and sexual size dimorphism in
675 wasps and bees. Behav. Ecol. Sociobiol. 62:843-852
676 Stearns SC (1977) The evolution of life-history traits: a critique of the
677 theory and a review of the data. Annu. Rev. Ecol. Evol. Syst. 8:145-171
678 Stephens PR, Wiens JJ (2009) Evolution of sexual size dimorphisms in
679 emydid turtles: ecological dimorphism, Rensch's rule, and sympatric
680 divergence. Evolution 63(4): 910-925.
681 Stillwell RC, Blanckenhorn WU, Teder T, Davidowitz G, Fox CW (2010)
682 Sex differences in phenotypic plasticity affect variation in sexual size

683 dimorphism in insects: from physiology to evolution. Annu. Rev.
684 Entomol. 55:227-245
685 Temeles EJ, Pan IL, Brennan JL, Horwitt JN (2000) Evidence for
686 ecological causation of sexual dimorphism in a hummingbird. Science
687 289(5478): 441-443
688 Tormos J, Asis JD, Gayubo SF (1995) Observations on the nesting
689 behaviour of *Ammophila laevicollis* Andre (Hymenoptera, Sphecidae).
690 Ann. Soc. Entomol. Fr. 31:157-163
691 Tornberg R, Mönkkönen M, Pahkala M (1999) Changes in diet and
692 morphology of Finnish goshawks from 1960s to 1990s. Oecologia,
693 121(3): 369-376
694 Trumbo ST (2012) Patterns of parental care in invertebrates. In: Royle
695 NJ, Smiseth PT, Kölliker M (Eds.) The evolution of parental care. Oxford
696 University Press, pp. 81-100
697 Weaving AJS (1988) Prey selection in several sympatric species of
698 *Ammophila* W. Kirby (Hymenoptera: Sphecidae) in southern Africa. Ann.
699 Cape Prov. Mus. (Nat. Hist.) 16:327-349
700 Weaving AJS (1989a) Nesting strategies in some southern African
701 species of *Ammophila* (Hymenoptera: Sphecidae). J. Nat. Hist. 23:1-16
702 Weaving AJS (1989b) Habitat Selection and Nest Construction Behavior
703 in Some Afro-Tropical Species of *Ammophila* (Hymenoptera, Sphecidae).
704 J. Nat. Hist. 23:847-871, doi:10.1080/00222938900770451
705 Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F
706 (2006) Sex-specific foraging behaviour in a seabird with reversed sexual
707 dimorphism: the red-footed booby. Oecologia 146(4): 681-691
708 Wheeler P, Greenwood PJ (1983) The evolution of reversed sexual
709 dimorphism in birds of prey. Oikos 40(1):145-149
710

711 Figure captions

712

713 **Fig. 1** Phylogeny of ammophiline digger wasps used in this study,
714 showing both extant and reconstructed ancestral states for the continuous
715 variables sexual size dimorphism (SSD; female weight/male weight) and
716 number of prey per offspring (PPO; midpoint value). Both SSD and PPO
717 values have been scaled from 0 to 1 to represent the minimum and
718 maximum in the dataset, respectively. Maximum likelihood ancestral
719 state reconstruction was carried out using the ace() function in the ape
720 package in R (Paradis et al 2004)

721

722 **Fig. 2** The relationship between $\log_{10}$(male weight) and log10(female
723 weight) for 21 species of ammophiline wasps. Open circles and dashed
724 line represent species that invariably provide one large prey item per
725 offspring (PPO=1), while filled circles and solid line represent species
726 that sometimes or always use more than one smaller prey item per
727 offspring (PPO>1). Dotted line represents the case where female size =
728 male size

729

730 **Fig. 3** The relationship between the number of prey provided per
731 offspring and untransformed sexual weight dimorphism, i.e. mean female
732 weight/mean male weight, for 21 species of ammophiline wasps. Lines
733 are from PGLS regression

734

735 **Fig. 4** Relationship between the number of prey provided per offspring by
736 21 species of ammophilines and residuals from regression of either (a, c)
737 $\log_{10}$(wing length) on log10(dry weight) or (b, d) $\log_{10}$(thorax length) on
738 $\log_{10}$(dry weight). (a) and (b) are for females (F) only, while (c) and (d)

739 are for males (M) only. Best-fitting PGLS regression lines are shown
740 when the relationship was statistically significant
741
742
743